SPECIES DIVERSITY OF ARACEAE IN COLOMBIA: A PRELIMINARY SURVEY[1]

Thomas B. Croat[2]

ABSTRACT

Species diversity of neotropical Araceae is greatest in northwestern South America along the Pacific slopes of the Andes in Colombia and adjacent regions of northern Ecuador. This region is the wettest part of the continent and has some of the largest tracts of relatively undisturbed forests. Colombia is the most species-rich area for Araceae. The family occurs virtually throughout the country, but is much more diverse from sea level to about 1,500 m in the Cordillera Occidental. Of the 15 study sites in Colombia, containing eight different Holdridge Life Zones, the most species-rich was the wettest life zone (premontane rainforest transition to tropical wet forest) at near sea level. Species diversity diminishes substantially at higher elevations even in very wet forests, but is moderately rich to at least 1,100 m. The Cordillera Central of Colombia is substantially drier, particularly during a certain part of the year, and has fewer, more widespread species. It is also the area most heavily disturbed. The Cordillera Oriental is the most poorly collected, but appears to be much less diverse in Araceae than the Cordillera Occidental. The one site studied on the eastern side of the Cordillera Oriental showed the presence of an Amazonian element in the flora. This, coupled with its complement of endemic species at higher and middle elevations, may be an indication that the eastern range will prove to be more species-rich than the central range of the Andes in Colombia.

MATERIALS AND METHODS

This study is based on a series of 15 one- or two-day single site surveys of different areas in Colombia between 1980 and 1990. Although the Araceae are poorly known in their totality, aroid species are generally easy to distinguish by aroid workers on a local basis. This familiarity enables species counts to be made on a site-by-site basis as a means of comparing species diversity between areas. This paper deals with such a study. The purpose of the study is to compare different parts of Colombia both in a general way for a variety of sites throughout the country and in a more specific way for two principal sites on the Pacific slope of the Cordillera Occidental. Voucher specimens are on deposit at the Missouri Botanical Garden. A list of the specific voucher numbers and their dates of collection may be obtained by contacting the author.

INTRODUCTION

The Araceae, a family of 106 genera (Croat, 1988), are taxonomically one of the most poorly known families of flowering plants in the Neotropics. The family has two major centers of diversity, with 32 genera in New World tropics and subtropics and 41 genera in the Old World tropics and subtropics. The total number of species is unknown, but is believed to exceed 3,500. About two-thirds of the species are believed to occur in tropical South America (Croat, 1979), and Colombia may have as many species as all the remaining parts of South America combined. The greatest uncertainty in species count is attributed to the poorly known status of the two largest genera in the family, *Anthurium* and *Philodendron*. The former is believed to have about 1,000 species and the latter approximately 700.

The Central American aroid flora is reasonably well known (Croat, 1981, 1983, 1986a, 1991) and comprises over 500 species. Species diversity in Central America increases as one approaches South America (Croat, 1986b). Using *Anthurium* as an example, Mexico has approximately 50 species, Guatemala 25, Honduras 20, Nicaragua 35, Costa Rica more than 80, and Panama about 160. No approximation is yet possible for Colombia, but certainly it has more species than all of Central America.

In contrast to Central America, many South American countries are poorly known floristically.

[1] This study was completed with support from National Geographic Society grant 4116-89 as well as National Science Foundation grants DEB80-11649, BSR83-06297, and BSR89-05890 and is based on field observations in Colombia between 1980 and 1990. Voucher specimens are in cultivation at the Missouri Botanical Garden for future extensive observations.

[2] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

Exceptions are Venezuela (Bunting, 1979; Croat & Lambert, 1986), Argentina (Crisci, 1971), and Paraguay (Croat & Mount, 1988). The Guianas (Guayana, Suriname, and French Guiana) and the lowland Amazonian basin are reasonably well known and contain moderately few new species (probably less than 5–10% of the total). In the case of the latter region, a large portion of the species are widespread, extending throughout the upper Amazonian drainage in Brazil and into the lowlands of Colombia, Ecuador, Peru, and Bolivia. Some species, such as *Philodendron melinonii* Brongn. and *Anthurium bonplandii* Bunting, even extend from the Guiana highlands into the northern Amazon basin. Because of the widespread nature of many of the species in the Amazon basin, the majority of the species occurring there were collected years ago by early explorers, including Spruce, Ule, Poeppig, and others, and were described by the early monographers of the family, H. W. Schott and A. Engler.

Considering its vast extent, the Amazonian basin is comparatively low in species diversity of Araceae. This is perhaps owing to the vast extent of tropical moist forest life zones in the region, which are seasonally too dry for good epiphyte development, and also because much of the area along rivers is annually flooded, sometimes for long periods of time. Madison (1979) reported that the Brazilian state of Amazonas, which encompasses 15% of the Amazon basin, for example, had only about 70 species. I believe that the entire lowland Amazonian basin has probably fewer than 150 species for areas under 150 m elevation.

Southeastern South America was also botanized early and extensively, especially by Glaziou, and many species were described. However, owing to the complex taxonomy of *Anthurium* sect. *Urospadix*, which makes up a large portion of the species in this region, the number of species there is still poorly known. In Brazil, Simon Mayo has made a detailed listing of the species of Araceae from Bahia (Mayo, pers. comm.), and though less species-rich, there is a treatment of the Araceae of Santa Catarina do Sul (Reitz, 1957). However, many portions of southeastern Brazil are still poorly known. The region is also among the most disturbed of all South America, with the state of São Paulo, for example, having only a small percentage of its land surface still forested. Most of the species from southeastern and eastern Brazil are endemic to the region, and relatively few occur also in the Amazonian basin. Species diversity in the Amazon basin increases dramatically to the west, especially as one approaches the Andes.

The highly dissected nature of the Andes has apparently led to great speciation there. Even relatively low elevations, such as the state of Acre in Brazil in the western perimeter of the Amazon basin are (perhaps owing to a rich layer of alluvium washed down from the Andes) richer in species than areas further to the east.

Endemism for Araceae is high in the Andean region, especially at middle elevations on both slopes of the Andes. This is generally true of all elevated regions of Central and South America. Endemism in *Anthurium* was discussed in detail for Central America (Croat, 1983, 1986a, and for *Anthurium* sect. *Pachyneurium*, Croat, 1991). Though the number of endemic species is greatest in the Andes of western South America, endemism is also high for the now much older, eroded mountains of eastern South America, including the Guiana highlands and the remnants in eastern and southeastern Brazil, south of the Amazon River (as was discussed above for *Anthurium* sect. *Urospadix*).

Species diversity in *Araceae* is comparatively high on both slopes of the Andes in northern South America, but diminishes dramatically south of Esmeraldas Province in Ecuador, especially in areas near the coast, owing to the effect of the Humboldt currents and the desertification created by the cool, dry air above it. No species of Araceae occur in Chile or in southern Argentina, despite the fact that some species occur at much higher latitudes in the Northern Hemisphere. Relatively few species occur in Peru west of the Andes, and these are represented either high in the mountains or at lower elevations only near the northern border of the country. The same is true for much of the southern part of Ecuador on the Pacific slope.

Geographical Diversity of Colombia

Colombia, with 1,138,914 km² (439,737 mi.²), is both large and geographically diverse. Though the Andes begin in southern Colombia as an apparently single massif, they split into three chains in Colombia, with the Cordillera Oriental and the Cordillera Central somewhat separated from the Cordillera Occidental and deflected to the east. The Cordillera Occidental extends northward relatively near the coast until it diminishes in northern Antioquia before reaching the Caribbean Sea. The Cordillera Central extends for about the same distance northward, somewhat parallel to the western range, and is delimited by the Río Cauca valley to the west and the Río Magdalena valley to the east. The Cordillera Oriental is deflected markedly to the northeast, includes a series of vast tablelands,

and extends all the way to the Venezuelan border. There it branches into the Cordillera de Mérida, which extends northeast into Venezuela, and the Serranía de Perijá, which extends north along the western Venezuelan border almost to the Caribbean.

The extensive modifications of the topography of Colombia by the elevation of the Andes have resulted in dramatically different climatic regions throughout the country. A total of 29 life zones in the Holdridge Life Zone System (Inst. Geogr. "Agustín Codazzi," 1977) exist in Colombia, and at least 15 of these contain Araceae. The Chocó Department contains eight life zones (Forero, 1982; Forero & Gentry, 1989), and all are rich in Araceae. These include tropical rainforest (bp-T, henceforth referred to as pluvial forest), premontane rainforest (bp-PM), tropical wet forest (bmh-T), premontane wet forest (bmh-PM), tropical moist forest (bh-T), lower montane rainforest (bp-MB), lower montane wet forest (bmh-MB) and montane rainforest (bp-M). Symbols are those used on the Holdridge Life Zone map published by Instituto Geográfico Agustín Codazzi (1977).

Forests along the Pacific slopes of the Andes receive the greatest rainfall, with up to 11,700 mm for various years at Tutunendo (Gentry, 1982). This village lies at ca. 90 m elevation between Quibdó and Bolívar in a region of premontane rainforest. The higher slopes are subject to afternoon fog resulting from the buildup of clouds as moisture accumulates in the atmosphere. Both the rainfall and the moisture-laden clouds increase atmospheric humidity to the extent that epiphytism is greatly enhanced.

Many areas of the Central Cordillera lie to some extent in rain shadows of moisture-laden air arriving off the Pacific Ocean to the west. The same is true for the eastern slopes of the Cordillera Occidental, which are much drier than the opposite slopes of the same mountain chain. These rain shadows affect not only the total amount of rainfall in the central mountain chain, but also the length of the dry season, which greatly diminishes the number of aroid species capable of surviving in the region. The Cordillera Central is much more degraded than the western range because of the drier conditions caused by rain-shadowing and also due to its close proximity to many of the country's larger population centers.

The Cordillera Oriental is more complex climatologically. Portions of the south and central part of the range are affected by rain-shadowing from blockage by the western and central range of mountains. Yet at the same time, the eastern range is affected by moisture-laden air from the Amazon basin. The lower, western slopes of the Cordillera Oriental are relatively dry, whereas the eastern slopes of the same chain are much wetter. To the north, however, the mountains of the eastern chain are affected by the moisture arriving from Lake Maracaibo as well as from the Caribbean Sea. Much of the Cordillera Oriental is degraded, especially in the central portions of the range near the large population centers, such as Bogotá and Bucaramanga. It was the focus of some of the earliest collecting in Colombia, but still remains the most poorly known area for Araceae. Parts of the range to the northeast of Bogotá are so cold and high as to develop true páramo, from which aroids are excluded.

Aroid Diversity in Colombia

With the possible exception of eastern Brazil, the region most poorly known floristically in South America is the slopes of the Andes in western South America. Species diversity is greatest in the wet tropical areas on both sides of the equator in Colombia, Ecuador, and Peru. The aroids are effectively eliminated from the Pacific slope of Peru and southern Ecuador owing to the Humboldt Current desertification, whereas Colombia is exceedingly rich on the very wet Pacific slope, leading to a much greater overall species diversity. This fact, coupled with the high rate of endemism in the family and the much more complex mountain system in Colombia, has created a situation where the aroid flora of this country is the highest of any region in the world. Parts of Ecuador are certainly as species-rich per unit area, but the country is much smaller and geographically less complex.

The South American Andes are poorly known owing to the large number of species occurring in the region and their taxonomic complexity. The genus *Philodendron* and some sections of *Anthurium* are particularly poorly known. Since these two genera may constitute 70–80% of the aroid flora, any given local flora may be very poorly known to the species level. Other complex and poorly known genera, especially at lower elevations, include *Dieffenbachia*, *Monstera*, *Rhodospatha*, and *Spathiphyllum*. *Stenospermation*, rich in species and even more poorly known, is particularly diverse at middle to high elevations in the Andes.

In all, 15 sites were studied throughout Colombia (Fig. 1). The sites included eight along or in the western range, five in the central range, and two in the eastern range. Both major study areas were

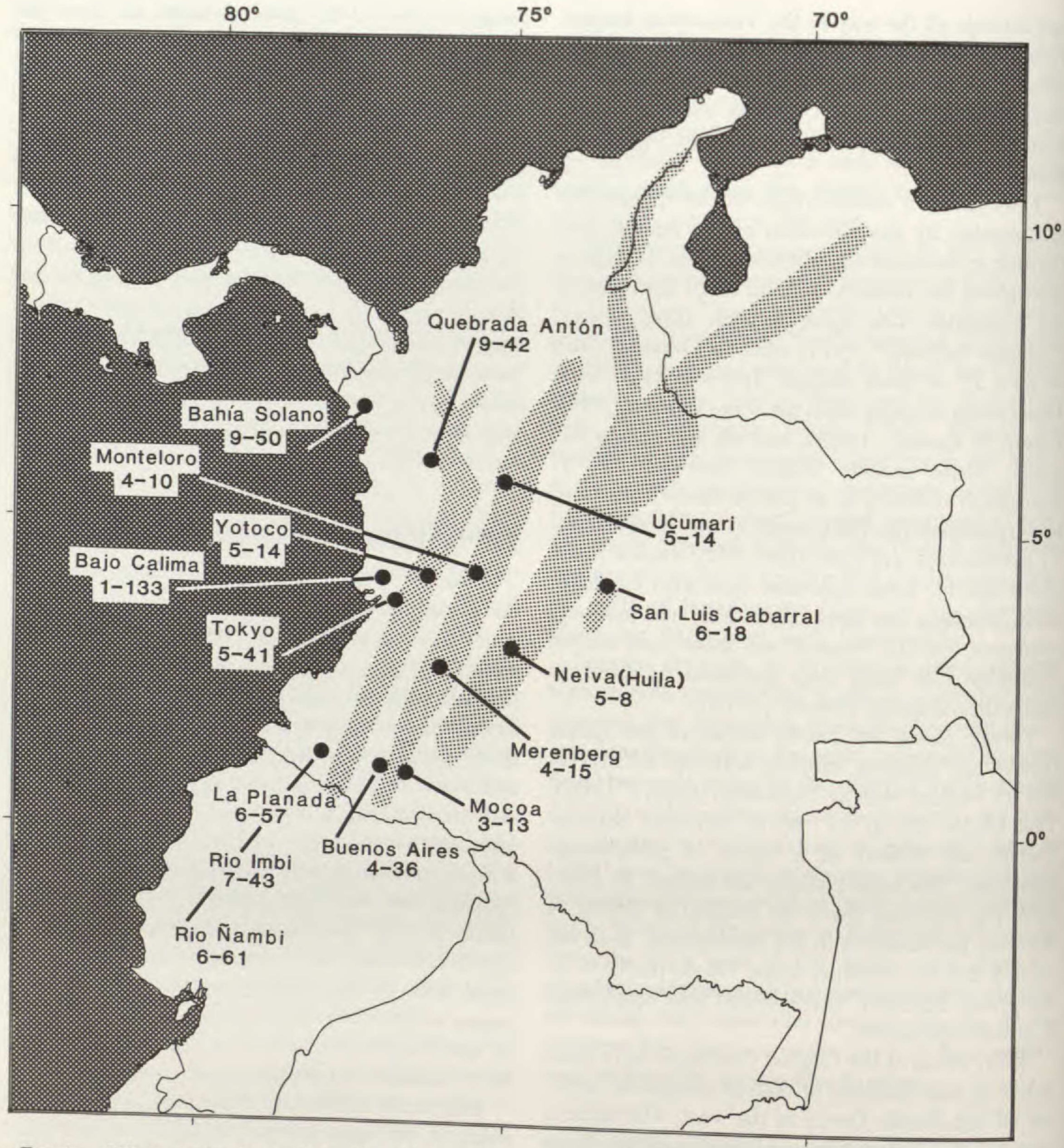

FIG. 1. Fifteen study sites in Colombia with number of genera and species collected. (Map prepared by J. Myers.)

in the Cordillera Occidental. Additional sites have been visited in the eastern range, but they were excluded either because it was deemed that they were not sufficiently natural or not enough time was spent in them to ensure a complete survey.

The study sites were diverse ecologically, ranging from very wet to moderately dry. The life zones included were: premontane rainforest transition to pluvial forest (1); tropical wet forest (2 sites); premontane wet forest (4); premontane rainforest (2); lower montane wet forest (1); lower montane rainforest (1); premontane moist forest (3); lower montane moist forest (1). The only major life zones with large numbers of Araceae that were not studied were tropical moist forest and pluvial rainforest.

Though the two major sites were extensively collected and the results probably come close to representing the total number of species for the sites, the remaining sites were collected for shorter periods of time, and in most cases these results would not be expected to represent the total count of species in the areas. Though the latter surveys are invalid statistically because the sites were not measured nor even deemed to be of equal size, they are believed to reflect accurately the species richness of the relative areas. The results of the

survey, I believe, show a true picture of the difference in species diversity in different parts of Colombia. Despite the presumed inaccuracy of the counts for total species in each area, they do reflect, in general terms, the trends for species diversity that are postulated.

Collecting sites were concentrated in the Cordillera Occidental owing to the greater diversity and the greater ease of access to undisturbed sites. In each case a serious attempt was made to collect every species present at each site, whether fertile or sterile. This was essential since at any one time only a small percentage of the flora is fertile. Because live material was collected in most cases for cultivation, future fertile parts will provide ultimate identification.

Discussion of the Study Sites

General Sites

Cordillera Occidental

(Low Elevations)

Bahía Solano. This is the northernmost site studied, situated at 6°14′N, 77°24′W near sea level in an area of tropical wet forest near the Pacific coast in Chocó Department. The survey netted nine genera and 50 species, but the forest near Bahía Solano is somewhat degraded and perhaps does not properly reflect the richness of the area.

Determined species from the area include *Anthurium formosum* Schott, *A. lancifolium* Schott, *A. obtusilobum* Schott, *A. ramonense* Engl. ex K. Krause, and *Rhodospatha moritziana* Schott.

Quebrada Antón. The site is situated at 5°20′30″N, 76°13′45″W in an area of premontane rainforest at about 240–250 m in the Department of Chocó near the border of Risaralda, along the road between Pueblo Rico, Risaralda, and Istmina, Chocó. Nine genera and 42 species were collected.

The taxa definitely determined to species from the site include *Anthurium formosum*, *A. ravenii* Croat & Baker, *A. warocqueanum* J. Moore, *Philodendron verrucosum* Mathieu ex Schott, *Rhodospatha moritziana*, *Stenospermation multiovulatum* (Engl.) N. E. Br., *Syngonium foreroanum* Croat, and *S. macrophyllum* Engl.

(Middle Elevations of Western Slope)

Microondas Tokyo. The site is at 3°30′N, 76°44′W in a region of premontane rainforest around a microwave station at 2,000 m in Valle Department, above the town of Queremal along the old road between Cali and Buenaventura. The study site yielded five genera and 41 species.

Identified species include *Anthurium panduriforme* Schott, *A. obtusilobum*, and *A. tenerum* Engl.

Río Imbi. This study site is located at 1°18′N, 78°04′W along the Río Imbi in the Department of Nariño near Ricaurte, in a somewhat degraded region of premontane wet forest at 1,100 m. It yielded seven genera and 43 species. Only a few of the species located here also occur at the La Planada study site, even though it is only 700 m lower in elevation and barely 7 km away from that latter site.

Known species include *Anthurium panduriforme*, *A. draconopterum* Sodiro, *A. obscurinervium* Croat, *A. myosuroides* (HBK) Endl., *A. scandens* (Aubl.) Engl., subsp. *pusillum* Sheffer, *Philodendron ecuadoriense* Engl., *P. inequilaterum* Liebm., and *P. verrucosum*.

Río Ñambí. This area is along the Río Ñambí in Nariño Department at 1°18′N, 78°04′W in a region of premontane wet forest at 1,100 m, west of Altaquer. Six genera and 61 species were collected. The region consists of virgin forest and showed surprisingly little floristic relationship to the Río Imbi site located only about 20 km to the northwest, at the same elevation and in the same life zone.

Identified species included *Anthurium draconopterum*, *Philodendron inequilaterum*, *P. verrucosum*, and *Xanthosoma daguense* Engl.

(Higher Elevations of Eastern Slope)

Parque Yotoco. This area is a reserve and one of the few remaining tracts of natural vegetation on the eastern slopes of the western massif. It is located in the Department of Valle in a region of premontane moist forest life zone at an elevation of about 1,500 m. The reserve is located along the main highway between Dapa and Loboguerrero at 3°52′N, 76°22′W.

The site contained five genera and 14 species; those identified are *Anthurium myosuroides* and *Xanthosoma daguense* Engl.

Cordillera Central

Five sites were studied in the central massif. The intermountain valleys to the east and west of the Cordillera Central are unknown, since most portions have been completely denuded for a long time. All of the sites studied were at moderately high elevations.

Parque Ucumarí. This is a preserve that lies

at 4°02′N, 75°30′W, southeast of the city of Pereira in the drainage of the Río Otun in the Department of Risaralda at 1,900–2,200 m elevation. It lies in a region of lower montane moist forest life zone and is relatively species-poor, owing to the high elevation, with only five genera and 14 species encountered. One of the species common at the site was *Anthurium longegeniculatum* Engl.

Monteloro. The study site is located at 3°55′N, 76°04′W, near the village of Monteloro in eastern Valle Department, in a region of premontane moist forest at 2,080–2,100 m elevation. The general region is much denuded, but the study site remains relatively undisturbed. It yielded only four genera and 10 species.

Anthurium myosuroides was common at the site. Another common, unknown, but distinctive *Anthurium* with cordate blades, a large red spathe, and a yellow-green spadix was also found at the next site, Reserva Merenberg.

Merenberg. The study site known as the Reserva Natural Finca Merenberg is located at 2°16′N, 76°12′W on the eastern slope of the Cordillera Central in the Department of Huila, in a region of lower montane wet forest at 2,300 m. The preserve was established by the owner, Gunter Buch, and the World Wildlife Fund. It was virtually the only remaining natural vegetation left in the region and netted only four genera and 15 species of Araceae.

Known species collected here included *Anthurium corrugatum* Sodiro, *A. longegeniculatum*, *A. microspadix* Schott, *A. scandens* (Aubl.) Engl., and *Chlorospatha longipodum* (K. Krause) Madison.

Buenos Aires. The area studied lies at 1°04′N, 76°48′W on the eastern side of the Cordillera Central in the Department of Putumayo, near the village of Buenos Aires, west of Mocoa, in a region of lower montane rainforest at about 2,500 m. Relatively large tracts of vegetation still exist in this area, but they are becoming rapidly disturbed. The vegetation consists of small trees and shrubs. Four genera and 36 species were found here; the only known species are *Anthurium longegeniculatum* and *A. scandens*.

Mocoa. The area studied lies along the Río Mocoa, near the town of Mocoa at 1°10′N, 76°33′W in Putumayo Department. It lies on the eastern side of the Cordillera Central in an area of premontane wet forest transition zone to tropical wet forest life zone at about 1,800 m. The site was relatively disturbed and yielded only three genera and 13 species.

The species known from the study site are *Anthurium alienatum* Schott, *A. harlingianum* Croat, *A. trinerve* Miq., *Philodendron inequilaterum*, *P. megalophyllum* Schott, and *P. panduriforme* Schott. All of these are widespread species in the Amazon basin.

Cordillera Oriental

Only two sites are included for the Cordillera Oriental, one located on the western slopes of the massif and one in the Cordillera de la Macarena, which is appropriately a part of the eastern range, though it rises substantially above all the surrounding terrain and is somewhat segregated from the rest of the Cordillera.

Neiva. The study site is located at 2°56–57′N, 75°0–7′W in the Department of Huila in the mountains to the east of the city of Neiva, in a region of premontane moist forest at 745–870 m. The region is somewhat disturbed and has a relatively marked dry season. It yielded only five genera and eight species.

Among the species were the widespread Amazonian species *Philodendron barrosoanum* Bunting and the even more widespread *Xanthosoma mexicanum* Liebm. Also occurring there were *Anthurium glaucospadix* Croat, which occurs on both sides of the Cordillera Central, and *A. nymphaeifolium* K. Koch & Bouché, a species with a generally more northern distribution in the eastern range, as well as the Cordillera de Mérida and Cordillera de la Costa in Venezuela.

San Luis de Cabarral. The study site was located at 3°45′N, 73°45′W, east of the village of Cabarral near the base of the Serranía de la Macarena in an area of tropical wet forest life zone at 530 m elevation. Six genera and 18 species were collected here. These included many widespread Amazonian species, but with some endemics as well. Species with an Amazonian distribution included *Anthurium acrobates* Sodiro, *A. fendleri* Schott, *A. pentaphyllum* (Aubl.) G. Don var. *pentaphyllum*, *Monstera gracilis* Engl., *M. lechleriana* Schott, *Philodendron acutatum* Schott, *P. barrosoanum*, *P. fragrantissimum* (Hook.) Kunth, *P. inequilaterum*, *P. ornatum* Schott, *P. wurdackii* Bunting, *Rhodospatha oblongata* Poeppig, *Spathiphyllum cannifolium* (Dryand.) Schott, and *Syngonium yurimaguense* Engl.

The forest was a remnant, and probably the low numbers do not properly reflect the total potential flora for the region.

SPECIFIC SITES

Two sites will be discussed separately because they represent areas now reasonably well known

in comparison to the general sites mentioned above. Both were in the Cordillera Occidental, so for the purposes of general conclusions regarding species diversity in Colombia their data will be incorporated with the general sites.

Bajo Calima. "Bajo Calima" refers generally to the lower Río Calima valley in the Department of Valle. More specifically, as defined here, it refers to the area south of the Río Calima near the Pacific Ocean. The study site is located at 3°57′–4°10′N and 77°01–12′W and is within the forestry concession of Cartón de Colombia. The assistance of the lumber company has been instrumental in the success of the survey. The forestry concession lies largely on a peninsula of land jutting out into the Pacific Ocean and separating the Bahía de Málaga to the north from the Bahía de Buenaventura to the south. It is just north of the coastal city of Buenaventura in Valle Department.

The region consists of a premontane rainforest in transition to pluvial forest. Elevations range from sea level to about 200 m, and drainage is to the north into the Río Calima, to the west into the Bahía de Málaga and to the south into the Bahía de Buenaventura. The overlying forest is dense, with most trees less than 60 cm in girth and less than 30 m in height. The understory vegetation is dense and light conditions are low. Most of the aroid species occur as epiphytes, but only rarely are they very high in the trees. Rainfall at Bajo Calima is usually late in the day or at night and usually begins as a light mist, often as early as 3:00 P.M. Heavier rains usually occur at night. Periods of rain are also common in the early morning. Total rainfall is recorded as 7,470 mm (Gentry, 1991). Rainfall is lowest from December to March (200–300 mm), with the lowest recorded monthly rainfall in January 1963 when only 139 mm fell. Annual temperatures average 27.3°C with a daily minimum of 21.4°C and a maximum of 30.3°C (Faber-Langendoen, 1989).

Species characteristic of the flora are *Anthurium brownei* Masters, *A. chlorocardium* Sodiro, *A. coclense* Croat, *A. insigne* Masters, *A. paludosum* Engl., *A. pluviaticum* R. E. Schultes, *A. trinerve*, *A. trisectum* Sodiro, *Philodendron grandipes* K. Krause, *P. inequilaterum*, *P. verrucosum*, *P. senatocarpium* Madison, *P. tripartitum* (Jacq.) Schott, *Spathiphyllum friedrichsthalii* Schott, *Stenospermation andreanum* Engl., and *Syngonium macrophyllum* Engl.

La Planada. The region is located at 1°08′N, 77°04′W at the Reserva Natural La Planada, a 3,200-ha biological reserve in the Municipio of Ricaurte in Nariño Department. It was established with the assistance of the World Wildlife Fund and operated by the Fundación para Educación Superior. Elevations range from 1,300 to 2,100 m, but most of the collections were made between 1,700 and 1,850 m. The area is classified as premontane wet forest on the Holdridge Life Zone map of Colombia. Its forest canopy is also relatively short, with trees mostly less than 20 m tall. The understory vegetation is even denser than at Bajo Calima, and a much larger percentage of the species occur in partly rotted debris that has accumulated on the ground. In contrast to Bajo Calima, which is generally quite hot, the temperature at La Planada is substantially cooler, with average temperatures ranging from 12° to 22° Celsius. Though mornings are usually clear, rains generally begin by late afternoon, as at Bajo Calima, and continue into the night. Average annual precipitation is more than 4,430 mm. Though rainfall is rarely heavy, the region is often beset with cloudy and rainy conditions that may persist for weeks at a time. The soil perhaps never dries out.

Species characteristic of the flora are *Anthurium carchiense* Croat, *A. microspadix*, *A. mindense* Sodiro, *A. ovatifolium* Engl., *A. scandens* subsp. *pusillum*, *Monstera adansonii* Schott, *M. lechleriana*, *Philodendron lehmannii* Engl., *Rhodospatha densinervia* Engl. & K. Krause, and *Xanthosoma sagittifolium* Schott.

FLORISTIC COMPARISON OF PRINCIPAL STUDY SITES AT BAJO CALIMA AND LA PLANADA

Differences at the generic level

Dramatic differences abound between the two major study sites, the most apparent being the much higher species diversity and generic diversity in the lowland site. With 133 species known, Bajo Calima has more than twice as many species as La Planada, with 57. Moreover, continued studies are likely to increase this difference even further since each succeeding trip to the lower site has added greater numbers of known species. Because of the dramatic difference in elevation, it is not surprising that not a single species is common to the two areas. Since both areas are very wet and lack any significant dry season, temperature is probably the primary reason for differences in species composition between the two sites.

The difference in temperature between the two areas is also likely to be the principal reason for the unequal generic composition (Table 1). Generic diversity is much less at the upland site, with five genera lacking altogether at La Planada. The genera present at Bajo Calima but lacking at La Plana-

TABLE 1. Species diversity in Colombia.

	Anthurium	*Caladium*	*Chlorospatha*	*Dieffenbachia*	*Dracontium*	*Heteropsis*	*Homalomena*	*Monstera*	*Philodendron*	*Rhodospatha*	*Spathiphyllum*	*Stenospermation*	*Syngonium*	*Xanthosoma*	Total
Western Cordillera															
Bahía Solano	26			3			1	1	13	2		2	1	1	50
Quebrada Antón	18		1	2	1				11	2		2	2	3	42
Bajo Calima	63	1	1	4				2	40	3	2	12	3	2	133
Microondas Tokyo	27							2	6			3		3	41
Parque Yotoco	5							1	6	1				1	14
La Planada	32							2	12	1		7		3	57
Río Imbi	19		2	1					17		1	2		1	43
Río Ñambí	26		1						23	3		6		2	61
Central Cordillera															
Ucumarí	10		1						1	1				1	14
Monteloro	7								1	1				1	10
Merenberg	11		1							2				1	15
Buenos Aires	17								12			1		6	36
Mocoa	4								8			1			13
Eastern Cordillera															
San Luis Cabarral	3							3	9	1	1		1		18
Neiva	2		1					1	3					1	8

da include *Caladium*, *Chlorospatha*, *Dieffenbachia*, *Spathiphyllum*, and *Syngonium*. These genera are all characteristically more abundant and diverse at lower than at higher elevations. Three of the genera (*Chlorospatha*, *Dieffenbachia*, and *Spathiphyllum*) lacking at the 1,800 m site of La Planada are common at the Río Imbi site, only a few kilometers away but at an elevation of 1,100 m.

Dracontium is widespread in Central America, with four species ranging from Mexico to Panama. It is moderately common in some areas of northern Venezuela, and at least one species, *D. loretense* K. Krause, is common in the upper Amazon basin in Peru and Ecuador. It has not been found at either of the principal study sites on the Pacific slope of Colombia. Although rare on the Pacific slope of South America, it is to be expected at Bajo Calima, since it has been collected in premontane rainforest at Quebrada Antón, one of the other study sites. *Dracontium* has also been found on the Pacific slope of Ecuador.

Another genus almost certain to turn up at Bajo Calima is *Homalomena*. It has been collected nearby at a similar elevation southwest of Buenaventura. Three species are known from Chocó, *H. wendlandii* Schott, *H. peltatum* Masters, and one new species.

The genus *Heteropsis* is rare on the Pacific coast of Colombia and was not found at any of the study sites. It is most common in the Amazon basin and in eastern Brazil. While it occurs in Central America in tropical moist forest as far north as Nicaragua, and in northern Colombia at low elevations, it is known on the Pacific slope of South America only in the region of San José Palmar at 930 m elevation in montane wet forest life zones, and in Ecuador in Esmeraldas and Los Ríos Departments in premontane rainforest. No collection has been seen from the central or eastern ranges of the country.

Other genera not found in the surveys that might have been expected were *Montrichardia* and *Urospatha*. Both of these genera occur normally at low elevations. *Montrichardia* has been collected only in northern Chocó Department in the Río Atrato basin, in the Atlantic watershed. Collections have been seen from the Río Atrato near Bojaya at 6°35′N, 76°52′W, ca. 100 km north of Quibdó, but it is not expected to be found in any of the study sites reported here.

Urospatha is most abundant in the Amazon basin. It is restricted to the Caribbean slope in Central America and has been collected in northeastern Venezuela (Monagas and Delta Amacuro). While the genus is common in southeastern Colombia in Vichada, Meta, and Vaupés, no collections have been made in northern Colombia or on the Pacific slope of Colombia.

The genus *Stenospermation* is common at Bajo Calima and La Planada, but its high diversity at Bajo Calima was not expected. In Central America the genus is not very abundant at elevations below 400 m, and then only in tropical wet forest. However, the Bajo Calima area, with 12 species already known, is surprisingly rich. *Stenopermation* species are generally true epiphytes and require very humid sites.

Another surprising feature of the Bajo Calima site is the number of species of typically epiphytic genera of Araceae that occur terrestrially there. This is particularly true in *Anthurium* sect. *Porphyrochitonium*, which only rarely occurs terrestrially in Central America.

The genus *Philodendron* is typically most diverse at lower elevations, and this difference is apparent in the comparison of the two major study sites. *Philodendron* was notably more diverse at Bajo Calima, with 40 species versus only 12 at La Planada. Since the flora of La Planada is less than half as rich in Araceae as Bajo Calima, *Anthurium* species at La Planada were relatively numerous, with a total of 32 species versus 62 at Bajo Calima.

The only genus at La Planada with more species than at Bajo Calima was *Xanthosoma*, with three versus two species, respectively.

Differences at the infrageneric level

In addition to the differences so evident in the generic composition of Bajo Calima and La Planada, differences are also apparent within genera. *Anthurium*, for example, which can be easily separated into taxonomic sections, shows unequal representation in the two areas (Table 2).

The sectional system of classification used here is a slightly modified version of that of Engler (1905). Modifications of Engler's system have been discussed by Croat & Sheffer (1983), which includes the definitions of the 19 sections and illustrations of most.

Anthurium sect. *Tetraspermium* is represented at Bajo Calima by *A. trinerve* and at La Planada by *A. scandens* subsp. *pusillum*, but so far as is known, the most common taxon in the section, *A. scandens* subsp. *scandens*, does not occur at either site. This is unusual, since it is one of the most widespread and common taxa in the family.

TABLE 2. Comparison of *Anthurium* sections at Bajo Calima and La Planada.

Sections of *Anthurium*	Number of species per section: Bajo Calima	La Planada
Belolonchium	0	4
Calomystrium	4	2
Cardiolonchium	1	0
Digittinervium	2	1
Pachyneurium	0	1
Polyneurium	11	8
Porphyrochitonium	27	6
Semaeophyllium	1	0
Tetraspermum	1	1
Xialophyllium	6	6
Section unknown (oblong blades)	4	1
Section unknown (cordate blades)	4	5

One of the most remarkable differences in the sectional distribution of *Anthurium* between the two sites was exhibited by section *Porphyrochitonium*, which has 27 species at Bajo Calima and only six at La Planada. This section has a wide distribution, but is concentrated largely at lower elevations along the Pacific slope of South America.

Not surprisingly, section *Pachyneurium* is absent from Bajo Calima. The section is absent from the entire wet Pacific slope, with the exception of one species of series *Multinervia* that occurs at La Planada and two species of series *Pachyneurium* that occur on the highest dry slopes, entering from the Cauca River valley to the east.

Section *Xialophyllium* is generally most well represented at higher elevations, but perhaps owing to the larger size of the area studied at Bajo Calima, the number of species at the two sites is equal, with six species at each site.

Section *Polyneurium* is well represented at both sites, the number of species being more or less proportional to the sizes of the respective floras, with 11 represented at Bajo Calima and eight at La Planada.

Anthurium sect. *Digittinervium* is generally more common at higher elevations, but two species were found at Bajo Calima versus one at La Planada.

Section *Cardiolonchium* occurs at both lower and middle elevations, but the section was found only at Bajo Calima, with one species, *Anthurium splendidum* W. Bull, having been discovered there

recently. This was the first herbarium collection of this species since the type was prepared in 1883.

Section *Calomystrium* was represented at both sites, but was not particularly rich at either, with four species at Bajo Calima and two at La Planada.

Anthurium sect. *Belolonchium*, typically occurring at high elevations, would not have been expected at Bajo Calima. Four species of this section occur at La Planada.

Section *Semaeophyllium*, with *Anthurium insigne*, was represented only at Bajo Calima. Both areas still have a share of species whose sectional classifications are not yet known. One group with oblong, epunctate blades, which does not fit into any of the currently described sections, has four species at Bajo Calima and one species at La Planada. Another unknown group with cordate, epunctate leaf blades has four species at Bajo Calima and five species at La Planada.

While it is not yet possible to separate the *Philodendron* species in the two study sites into infrageneric taxonomic groups (with the exception of members of subg. *Pteromischum*), it is possible to separate them into scandent or appressed-climbing plants. Both groups are hemiepiphytic. No truly epiphytic *Philodendron* species occur at either site. At Bajo Calima there are 22 appressed climbers versus 14 vines. Two of the scandent plants were members of subgenus *Pteromischum*.

At La Planada five of the species were appressed epiphytes and six were vines. Only one of the latter group was in subgenus *Pteromischum*.

COMPARISON OF MAJOR MOUNTAIN SYSTEMS IN COLOMBIA

Though there are obvious differences in the quality of the sites in the different ranges (western, central, and eastern) owing to differences in size of the sites and their state of preservation, a general trend is clear. The wetter sites of the Cordillera Occidental yield much higher species totals than do the more mesic sites of the Cordillera Central and Cordillera Oriental. The eight sites in the western range averaged 55 species, whereas all sites in the central and eastern ranges averaged about 14 species. The number of species ranged from 14 to 133 species in the western ranges versus eight to 36 in the combined central and eastern ranges.

Philodendron averaged about 16 species per site for the eight study sites in the western range (ranging from six to 40 species per site) versus about five species per site (ranging from zero to 12) for the seven in the combined central and eastern ranges.

Anthurium averages about 27 species (ranging from five to 63) per site for the study sites in the western ranges versus an average of about eight (ranging from two to 17) in the central and eastern ranges.

Four genera were not represented at all in any of the sites of the central and eastern ranges. These were *Caladium*, *Chlorospatha*, *Dracontium*, and *Homalomena*. In addition, *Dieffenbachia* was rare, having been collected only at Neiva on the western slopes of the Cordillera Oriental.

Dracontium occurs on the wet Pacific slope of Colombia and Ecuador, in Venezuela, and throughout much of the Amazon basin, but I have seen no collections from the intermountain valleys in the Cordillera Central or Cordillera Oriental. Since it often occurs in seasonal habits, it is curious that it appears not to have been collected in these regions where numerous appropriate habitats occur. Probably the elevations in these regions are too high. Elsewhere the genus occurs mostly below 600 m elevation.

COMPARISONS OF STUDY SITES WITHIN THE CORDILLERA OCCIDENTAL

Because the study sites in the western range were more numerous and more diverse, some comparisons can be made among them. Although the detailed comparisons of the premontane pluvial forest lowland site at Bajo Calima and the premontane wet forest highland site at La Planada have shown conclusively that species diversity is much greater in the low, warmer site than in the higher, cool site, a comparison of the general lowland and middle elevation sites of the Pacific slope does not conclusively show where species diversity is greatest. Generally, the middle elevation sites were about as species-rich or more so than the sites at lowest elevations.

At the highest elevation sites *Philodendron* was usually dramatically less diverse than *Anthurium*, usually much less than one-half as diverse. At 1,800 m elevation at La Planada, there were 32 species of *Anthurium* versus only 12 species of *Philodendron*, and the Microondas Tokyo site at 2,000 m had 27 versus six species. In contrast, the low elevation sites of Bajo Calima, with 63 *Anthurium* versus 40 *Philodendron*, Bahía Solano (26 vs. 23 species), and Quebrada Antón (18 vs. 11 species) showed that *Philodendron* had one-half to three-quarters the total number of species as *Anthurium*.

In contrast, the middle elevations of 1,100 m

at the Río Imbi and the Río Ñambí yielded almost as many *Philodendron* species as *Anthurium*, with 19 *Anthurium* versus 17 *Philodendron* and 26 *Anthurium* versus 23 *Philodendron*, respectively. The Yotoco site at 1,500 m showed even more *Philodendron* than *Anthurium* species, with six versus five species, respectively.

The Yotoco site, the only collecting area on the eastern slope of the western range, was enlightening in another respect. The eastern slopes of the western range of the Andes have a severe dry season and also suffer diminished rainfall as the result of rain-shadowing. The Yotoco site is located near the summit on the eastern slope in premontane moist forest and is substantially drier than the other sites on the Pacific slope of the western range. The study area at Yotoco yielded only 14 species, far fewer than any of those sites on the western slope. It also had only five species of *Anthurium*.

The generally higher number of *Anthurium* versus *Philodendron* species at the highest elevations usually also holds in the central and eastern ranges, where most of the sites were above 2,000 m. For example, the number of *Anthurium* versus *Philodendron* species was 10 versus one at Ucumarí, seven versus one at Monteloro, 11 versus two at Merenberg, and three versus none at Neiva. However, the Buenos Aires site has 17 *Anthurium* versus 12 *Philodendron*. Mocoa, located nearby, had four *Anthurium* versus eight *Philodendron*. The lowland site on the eastern slope of the eastern range at the margin of the Amazonian lowlands had twice as many *Philodendron* as *Anthurium*.

Conclusions

These preliminary studies of species diversity in Colombia have shown interesting phytogeographic patterns. Remarkable differences are shown between different sites in different life zones and at different elevations. Though the surveys were inadequate to show conclusively which life zones might be richest in Araceae, evidence seems to point clearly to the wettest sites at low elevations. These sites were more diverse than those at high elevations. Study sites in the Cordillera Occidental also appear to be more species-rich than those in the central and eastern ranges.

Perhaps the most surprising finding in the study was the degree to which some sites in close proximity showed little overlap in species composition. For example, the Río Imbi site only a few kilometers away from La Planada and also in premontane wet forest shared few species with La Planada. Even more surprising, the Río Ñambí site, located relatively near Río Imbi in the same life zone and at the same elevation, shared few species with Río Imbi.

Future studies will involve more sites in the Cordillera Central and the Cordillera Oriental to confirm that they are less species-rich. More importantly, lowland sites in pluvial forest will be studied, since I believe that these will prove to be even richer than those of the premontane rainforest with transition to pluvial forest. Plans have been made to make a series of collections at different sites encompassing tropical wet forest, pluvial forest, premontane rainforest, and premontane wet forest in the Department of Nariño. The same will be done in the Department of Valle, where there is a series of reserves between the Pacific Ocean and the Continental Divide. Future studies will also be carried out at a number of sites in the Department of Cauca. These studies should indicate in which life zones species diversity is greatest and the extent of overlap in species composition at different sites. It is hoped that by means of these studies a better picture will emerge of the nature of speciation of the Araceae in this, the richest area on earth for aroid diversity.

Literature Cited

Bunting, G. S. 1979. Synopsis de las Araceae de Venezuela. Revista Fac. Agron. (Maracay) 10: 139–290.

Crisci, J. V. 1971. Araceae: Flora Argentina, Revista Mus. La Plata, Secc. Bot. 11: 193–284.

Croat, T. B. 1979. The distribution of the Araceae. Pp. 291–308 *in* K. Larsen & L. B. Holm-Nielsen (editors), Tropical Botany. Academic Press, London.

———. 1981. A revision of the genus *Syngonium* (Araceae). Ann. Missouri Bot. Gard. 68: 565–651.

———. 1983. A revision of the genus *Anthurium* (Araceae) of Mexico and Central America. Part I: Mexico and Middle America. Ann. Missouri Bot. Gard. 70: 211–240.

———. 1986a. A revision of the genus *Anthurium* (Araceae) of Mexico and Central America. Part II: Panama. Monogr. Syst. Bot. Missouri Bot. Gard. 14.

———. 1986b. Distribution of *Anthurium* in Central America. Selbyana 9: 944–999.

———. 1988 (1991). Ecology and Life Forms of Araceae. Aroideana 11(3–4): 4.

———. 1991. A revision of *Anthurium* section *Pachyneurium*. Ann. Missouri Bot. Gard. 78: 539–855.

——— & N. Lambert. 1986. Araceae of Venezuela. Aroideana 9: 3–213.

——— & D. Mount. 1988. Araceae. Pp. 1–45 *in* R. Spichiger (editor), Flora del Paraguay. Conservatoire botanique Genève & Missouri Botanical Garden. Imprimeries Populaires, Genève.

——— & R. D. Sheffer. 1983. The sectional groupings of *Anthurium* (Araceae). Aroideana 6: 85–123.

Engler, A. 1905. Araceae–Pothoideae. *In:* A. Engler, Das Pflanzenreich. IV. 23B: 1–330 (Heft 21).

FABER-LANGENDOEN, D. 1989. Combining Conservation and Forestry in a Colombian Rain Forest: An Ecological Assessment. Ph.D. Thesis. Saint Louis University, St. Louis, Missouri.

FORERO, E. 1982. La flora y vegetación del Chocó y sus relaciones fitogeográficos. Colombia Geográfica 10: 77–90.

——— & A. H. GENTRY. 1989. Lista anotada de las plantas del Departamento de Chocó, Colombia. Instituto de Ciencias Naturales, Museo de Historia Natural. Biblioteca José Jerónimo Triana no. 10.

GENTRY, A. H. 1982. Evidence for phytogeographic patterns as evidence for a Chocó refuge. Pp. 112–136 *in* G. T. Prance (editor), Biological Diversification in the Tropics. Colombia Univ. Press, New York.

———. 1991. The distribution and evolution of climbing plants. *In:* F. Putz & H. Mooney (editors), Biology of Vines. Cambridge Univ. Press, New York (in press).

INSTITUTO GEOGRÁFICO "AGUSTÍN CODAZZI." 1977. Zonas de vida o formaciones vegetales de Colombia. Memória explicativa sobre el Mapa Ecológico, Bogotá.

MADISON, M. T. 1979. Some notes on the aroids along the Rio Negro, Brazil. Aroideana 2: 67–77.

REITZ, P. R. 1957. Aráceas catarinensis. Sellowia 8: 20–70.